STUDIES ON THE TREMATODES OF WOODS HOLE

II. The Life Cycle of Stephanostomum tenue (Linton) [1]

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This paper deals with the results of a study of a member of the trematode family Acanthocolpidae obtained during the summers of 1936 and 1938 at the Marine Biological Laboratory at Woods Hole, Mass. No previous experimental work has been done on the life cycles in this family, and consequently the systematic relationships have been in question. This paper throws some light on these problems. The results obtained may be of some economic importance because the adult members of this family are parasitic in marine fishes, several of which are food fishes.

A synopsis of this work was given before the American Society of Parasitologists at the 1938 meeting at Richmond, Virginia.

Historical

Some of the members of the family Acanthocolpidae were at first assigned to the old pseudogenus, *Distomum*, and, due to the presence of spines encircling the mouth, were thought to be related to the echinostomes. Nicoll (1915) placed some of the acanthocolpids in the family Allocreadiidae because of the similarity in the arrangement of the reproductive organs in the two groups. Winfield (1929) criticizes Nicoll's classification, stating, "The Stephanochasminae should be excluded (from the Allocreadiidae) because of the Y-shaped excretory bladder, the circle of head spines, and the armed cirrus and vagina." The family name, Acanthocolpidae, was created by Lühe in 1909 to include trematodes whose principal diagnostic characters are: a well-developed prepharynx and pharynx, a very short esophagus, a Y-shaped excretory bladder, the ovary in front of the testes, the uterus between the ovary and the ventral sucker, the cirrus and vagina armed with spines, and the genital opening medially located anterior to the ventral sucker. At present the following seven genera are included in the family: *Stephanostomum* Looss 1899, *Dihemistephanus* Looss 1901, *Deropristis* Odhner 1902, *Acanthocolpus* Odhner 1905,

[1] This work was made possible through the use of the laboratory facilities maintained by Purdue University at the Marine Biological Laboratory.

Acanthopsolus Lühe 1906, *Tormopsolus* Poche 1925, and *Echinostephanus* Yamaguti 1934. Because of the presence of connections between the excretory bladder and the ceca in the genus *Echinostephanus*, Yamaguti separated it from the genus *Stephanostomum*. However, McFarlane (1936) described such connections in *Stephanostomum casum* (Linton) and indications of them in *S. tristephanum*. This suggests that a more extensive and intensive study of this character is needed.

Reports of observations pertaining to the life cycles of members of this family have appeared from time to time. Lebour (1907) described a cercaria that developed in rediae in the limpet, *Patella vulgata*, which she believed to be the larval form of some member of the genus *Stephanostomum*. However, this cercaria lacked eyespots, had a long esophagus and a small sac-shaped excretory bladder, all of which were contrary to observations on the adult worms. The same author (1910) described a cercaria from *Buccinum undatum* which she thought was the larval form of *Acanthopsolus lageniformis*. This cercaria possessed eyespots and general characteristics which agreed with the structures of the adult. No experimental work was done to test the validity of her assumption. Some of the cercariae had tails while the majority did not, which, in conjunction with the absence of large glands in the body, was interpreted by Lebour to indicate that no second intermediate host was required. This seems questionable since Linton (1898), Stafford (1904), Lühe (1906), Nicoll and Small (1909), Nicoll (1910), and others have found metacercariae of this family in various species of fishes. Linton (1898) found cysts of *Distomum valdeinflatum* attached to the peritoneum of *Alutera schoepfi* and *Menidia menidia notata*. Stafford (1904) found the cysts of *Stephanochasmus histrix* on the fins of *Pseudopleuronectes americanus*. Lühe (1906) found *Stephanochasmus ceylonicus* encysted in the subcutaneous tissue of *Narcine timlei* taken off Dutch Bay, Ceylon. Lebour (1907) reported *Stephanochasmus metacercariae*, probably *S. baccatus*, under the skin of the dab, witch, and long rough dab. Nicoll and Small (1909) discovered the cysts of *Stephanochasmus baccatus* under the skin of *Pleuronectes limanda*. They state, "It is not at all improbable that the cercariae of *S. caducus*, *S. triglae*, and *S. baccatus* are all to be found encysted in young pleuronectid fishes." Nicoll (1910) reported finding cysts of *S. baccatus* in *Drepanopsetta platessoides*. Yamaguti (1934) found cysts of *Stephanochasmus sp.* with 46 collar spines in *Lotella physis* and *Engraulis japonica*, *S. sp.* with 36 collar spines in *Argentina kagoshimae*, and *S. sp.* with 54 collar spines in *Bothrocara zesta* and *Furcimarius sp.* He also found *Echinostephanus* *sp.* with 40 collar spines encysted in the flesh of *Argentina kagoshimae.* The same author (1937) reported *Stephanochasmus bicoronatus* cysts in the body cavity of *Acanthogobius hasta* and on the gills of *Sciaena sp.* and *Taenioides lacepedi; Echinostephanus hispidis* cysts in the flesh of *Pseudorhombus pentophthalmus* and *Neopercis sexfasciatus* and *Tormopsolus* larvae encysted near the gills of *Leiognathus rivulata.*

Material and Methods

The snail, *Nassa obsoleta*, which serves as the first intermediate host, *Menidia menidia notata* the second intermediate host, and the puffer, *Spheroides maculatus*, which serves as the experimental definitive host, were all collected in the vicinity of Woods Hole. Naturally infected snails were used as sources of cercariae. Some *Menidia* and *Spheroides* were used for experimental feedings while others were retained as controls.

Living material was used in the study of many of the cercarial structures. Bouin's solution and a saturated aqueous solution of mercuric chloride were used as fixatives. Mayer's paracarmine was used to stain toto mounts, while sectioned material was stained with Ehrlich's hematoxylin. Infected snails, isolated in finger bowls filled with sea water, furnished a plentiful supply of cercariae for the experimental infection of *Menidia.*

Observations and Descriptions

The life cycle of *Stephanostomum tenue* involves the production of rediae and cercariae in the digestive gland of the marine snail, *Nassa obsoleta*, the development of the metacercariae in cysts in the liver of the small fish, *Menidia menidia notata*, and the maturation of the worm in the intestine of the puffer, *Spheroides maculatus.*

All measurements listed in this paper are expressed in millimeters.

The Redia (Figs. 3 and 4)

Natural infections of this trematode were found in about .4 per cent of the several thousand *Nassa obsoleta* under observation. Some increase in the number of infected snails in the latter part of the summer was noted, which may be correlated with the migratory habits of the hosts of the adult worms. The redia is an elongate, saccular structure with a pharynx and short rhabdocoel gut. The length of the gut, however, varies with age since it is nearly two-thirds the length of the very young redia (Fig. 4). The young redia also exhibits marked motility. The length of the redia varies from 0.14 to 0.66 with an average of about 0.5; the width varies from 0.03 to 0.14 with an average of about 0.10. The pharynx varies from about 0.025 long by 0.028 wide to 0.052 long by 0.029 wide. The number of germ balls and cercariae per redia varies from 0 to 14 for the former and 0 to 5 for the latter. No ambulatory processes were present and no birth pore was observed.

The Cercaria (*Fig. 1*)

The cercaria is of the ophthalmoxiphidio type with a simple tail. In swimming the tail is lashed back and forth while the body is held almost straight. In finger bowls of sea water the cercariae swim about for a short time and then settle to the bottom to which they adhere by the tips of their tails. No special glandular bodies were found in the distal region of the tail that might account for this adhesive action. This behavior may be of importance in the completion of the life cycle since the cercariae may become attached to food particles and may be eaten by fishes. The cercaria exhibits a positive response to light.

The cuticula of the body is spinous with larger spines on the anterior end. In addition to the spines there are seven or eight setae projecting from each side of the body. These are irregularly spaced along the entire body length. The oral sucker bears two rows (of 21 each) of alternating large spines about 0.005 long. These spines are easily detached under even slight cover-glass pressure. The body length varies with the degree of contraction from 0.145 to 0.38 with an average of 0.24, while the body width varies from 0.045 to 0.086 with an average of 0.064. The tail averages about 0.183 long by 0.031 wide. The oral sucker averages about 0.031 long by 0.030 wide while the ventral sucker averages about 0.033 long by 0.030 wide. The ventral sucker bears two rows of small papillae with about 65 papillae in each row. Projecting anteriorly above the oral sucker there is a simple spear-shaped stylet about 0.014 long. The mouth

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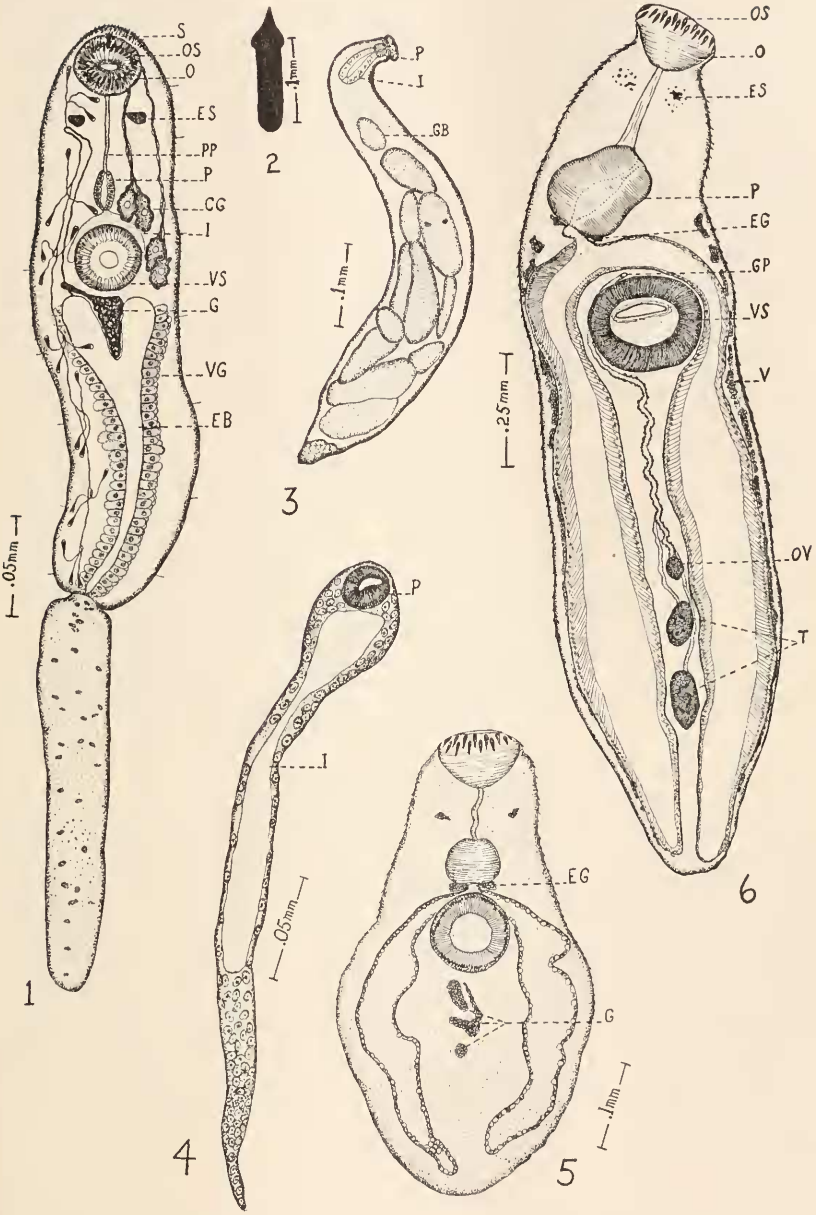
EXPLANATION OF PLATE

All drawings were made with the aid of a camera lucida. Abbreviations used: *CG*, cephalic gland; *EB*, excretory bladder; *EG*, esophageal gland; *ES*, eyespot; *G*, genital anlage; *GB*, germ ball; *GP*, genital pore; *I*, intestine; *O*, oral sucker; *OS*, oral spines; *OV*, ovary; *P*, pharynx; *PP*, prepharynx; *S*, stylet; *T*, testes; *V*, vitellaria; *VG*, vesicular gland; *VS*, ventral sucker.

FIG. 1. Ventral view of cercaria.
FIG. 2. Stylet of cercaria.
FIG. 3. Redia with germ balls and cercaria.
FIG. 4. Young redia showing elongate intestine.
FIG. 5. Metacercaria.
FIG. 6. Adult.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opens into a long narrow prepharynx approximately 0.038 long. The pharynx is subglobular and measures about 0.012 in length and width. The esophagus is extremely short. The rudimentary intestine branches just anterior to the ventral sucker and the branches do not extend beyond this organ. Two conspicuous eyespots are located, one on each side of the body, near the oral sucker. Four cephalic glands are located on each side of the body immediately lateral and anterior to the ventral sucker. On each side of the body the ducts from two glands pass anteriad median to the eyespot while the ducts from the other two glands pass anteriad lateral to the eyespot. The ducts of all four glands open to the exterior at the anterior end of the body. Other glands include numerous vesicular glands along the wall of the excretory bladder. The weakly Y-shaped excretory bladder extends almost to the ventral sucker. In some specimens the anterior wall of the bladder has a scalloped appearance. The main collecting ducts arise from the anterior margin of the excretory bladder and pass anteriad to the level of the eyespots where they bend on themselves and pass posteriad to supply both sides of the body. The flame cells are in seven groups of threes, with the first group given off just after the main duct bends posteriorly at the eyespot level. The other groups are given off at intervals along the side of the body.

The reproductive system is represented by a mass of deeply staining cells located just posterior to the ventral sucker and partially surrounded by the anterior wall of the excretory bladder.

The Metacercaria (*Fig. 5*)

The cercariae are taken into the digestive tract of the second intermediate host, *Menidia menidia notata*, where they work their way through the intestinal wall and encyst in the liver or mesenteries. No cercariae were observed to penetrate the bodies of the fishes through the skin. The metacercaria increases to several times the size of the cercaria. The 42 collar spines also increase in size until they are approximately 0.050 long. The eyespots and the glandular cells surrounding the excretory bladder undergo disintegration. There is a marked increase in the size of the pharynx. The branches of the intestine develop until they reach to near the posterior end of the body. The metacercaria is held within a rather tough, loose encystment sac.

The Adult (*Fig. 6*)

Nearly mature adult worms were obtained by feeding pieces of *Menidia* liver containing metacercariae to young puffers, *Spheroides maculatus*. The puffers were examined about two weeks after the initial feeding and the worms were recovered from the intestine. Remnants of the eyespots were still present. The oral spines were the same in number and approximately of the same size as in the metacercaria. The relative proportions of the suckers and the pharynx were about the same as in the metacercaria. Advances in development over the conditions found in the metacercaria are: the differentiated testes and ovary located in the posterior one-third of the body, the reproductive tubes extending from these organs to the genital pore located on the mid-ventral side of the body immediately anterior to the ventral sucker, and the small clusters of vitelline cells extending along the sides of the body from the posterior end of the pharynx to near the posterior end of the body. Complete functional maturity of the reproductive systems had not been attained since no eggs had been produced.

The following measurements and description are based on but a few worms so that the range of variation is probably less than would be found with a larger number of individuals. Body length 1.9 to 2.2, width 0.5; oral sucker 0.13 long by 0.18 wide; ventral sucker 0.22 long by 0.25 wide; prepharynx from 0.19 to 0.31 in length by about 0.015 in width near the oral sucker to 0.031 at its widest point near the pharynx; pharynx about 0.22 long by 0.16 to 0.18 in width; esophagus 0.04 to 0.07 long; ovary about 0.057 long by 0.03 to 0.038 wide; anterior testis 0.10 to 0.136 long by 0.04 to 0.07 wide, posterior testis 0.09 to 0.14 long by 0.04 to 0.07 wide.

Linton (1898) described *Distomum tenue* from the rectum of the striped bass, *Roccus lineatus*, collected at Woods Hole. The description he gave, with measurements in millimeters, is as follows: oral spines 0.051 long by 0.018 wide at base; esophagus 0.44 long by 0.34 wide (he undoubtedly has used the term esophagus for the pharynx); vitellaria voluminous, peripheral in the posterior region; genital aperture immediately in front of the ventral sucker; ova not numerous and comparatively large, lying close behind the ventral sucker; ova length 0.088, width 0.044; body length 2.9, width 0.28; diameter of oral sucker 0.26, of ventral sucker 0.38.

Discussion and Conclusions

Most descriptions of the adult members of this family show them to have remnants of eyespots. This may indicate that the family represents a fairly compact, closely related group. When the excretory bladder is mentioned at all in the descriptions of species, it is described as Y-shaped. However, in my study of living specimens of *Deropristis inflata*, a simple tubular or sac-shaped bladder was found.

There is very little in the literature on the rest of the excretory system although Pratt (1916) in his description of *Stephanochasmus casum* showed that the main collecting tubes pass anteriad to near the level of the eyespots without giving off secondary tubes.

The arrangement of the reproductive organs in the family Acanthocolpidae, as was pointed out by Nicoll (1915), is similar to the arrangement of these organs in the family Allocreadiidae. There is also some suggestion of similarity in the excretory systems of these two groups. In addition, the members of both families are primarily parasites of fishes. This suggests a rather close relationship between the two families. However, the elucidation of the life cycles of other genera is needed before a positive statement can be made.

The family Acanthocolpidae seems to be cosmopolitan in distribution since some of its members have been found in European, Greenland, North American, Japanese, and Ceylonese waters.

There has been some confusion in the literature concerning the generic name *Stephanostomum*. This confusion resulted from Looss' first (1899) naming the genus *Stephanostomum* and then changing it to *Stephanochasmus* (1900) because of its similarity to the genus *Stephanostoma* Danielson and Koren, a genus of Gephyrean worms.

Summary

It was found that the life cycle of *Stephanostomum tenue* involves the development of rediae and cercariae in the marine snail, *Nassa obsoleta*, the utilization of the small fish, *Menidia menidia notata*, as the second intermediate host, and the development of the adult worm in the intestine of the puffer, *Spheroides maculatus*. Although the puffer may serve as the experimental definitive host, the striped bass, *Roccus lineatus*, is probably a natural one.

About .4 per cent of the *Nassa obsoleta* observed were infected with this parasite.

The excretory system of the cercaria is represented by the formula $2[3+3+3+3+3+3+3]$.

The arrangement of the reproductive organs, some similarity in the excretory systems, and the fact that fishes serve as hosts to the adult worms suggest an affinity of the Acanthocolpidae to the family Allocreadiidae.

LITERATURE CITED

Lebour, Marie V., 1907. Fish trematodes of the Northumberland coast. Northumberland Sea Fish. Rep. 23–67.

Lebour, Marie V., 1910. Acanthopsolus lageniformis n. sp., a trematode in the catfish. Northumberland Sea Fish. Comm. Rep. 1909–1910, pp. 29–35.

Linton, E., 1898. Notes on trematode parasites of fishes. *Proc. U. S. Nat. Mus.*, **20**: 507–548.

Looss, A., 1899. Weitere Beiträge zur Kenntniss der Trematodenfauna Aegyptens, zugleich Versuch einer natürlichen Gliederung des Genus Distomum Retzius. *Zool. Jahrb. Abt. Syst.*, **12**: 521–784.

Looss, A., 1900. Nachträgliche Bemerkungen zu den Namen der von mir vorgeschlagenen Distomidengattungen. *Zool. Anz.*, **23**: 601–608.

Looss, A., 1901. Ueber die Fasciolidengenera Stephanochasmus, Acanthochasmus und einige andere. *Centralbl. Bakt. Parasit.*, **29**: 595–606, 628–634, 654–661.

Lühe, Max, 1906. Trematode parasites from the marine fishes of Ceylon. Ceylon Pearl Oyster Fish. and Marine Biol., Pt. 5: 97–108.

Lühe, Max, 1909. Parasitische Plattwürmer 17. I. Trematodes. In A. Brauer's, Die Süsswasserfauna Deutschlands.

Martin, W. E., 1938. The life cycle of Stephanostomum tenue (Linton), family Acanthocolpidae. (Abstract.) *Jour. Parasitol.*, **24** (Supplement): 27.

McFarlane, S. H., 1936. A study of the endoparasitic trematodes from marine fishes of Departure Bay, B.C. *Jour. Biol. Bd. Canada*, **2**: 335–347.

Nicoll, Wm., 1910. On the entozoa of fishes from the Firth of Clyde. *Parasitol.*, **3**: 322–359.

Nicoll, Wm., 1915. A list of the trematode parasites of British marine fishes. *Parasitol.*, **7**: 339–378.

Nicoll, Wm., and Wm. Small, 1909. Notes on larval trematodes. *Ann. Mag. Nat. Hist.* (*Ser. 8*), **3**: 237–246.

Odhner, Th., 1902. Mittheilungen sur Kenntniss der Distomen. II. Drei neue Distomen aus der Gallenblase von Nilfischen. *Centralbl. Bakter. Orig.* (4) **31**: 152–162.

Odhner, Th., 1905. Die Trematoden des arktischen Gebietes. *Fauna Arctica*, (2) **4**: 291–372.

Poche, Franz, 1925. Das System der Platoderia. *Arch. Naturg.*, **91**: 1–458.

Pratt, H. S., 1916. The trematode genus Stephanochasmus Looss in the Gulf of Mexico. *Parasitol.*, **8**: 229–238.

Stafford, J., 1904. Trematodes from Canadian fishes. *Zool. Anz.*, **27**: 481–495.

Winfield, G. F., 1929. Plesiocreadium typicum, a new trematode from Amia calva. *Jour. Parasitol.*, **16**: 81–87.

Yamaguti, S., 1934. Studies on the helminth fauna of Japan. Pt. 2. *Jap. Jour. Zoöl.*, **5**: 249–541.

Yamaguti, S., 1937. Studies on the helminth fauna of Japan. Pt. 20. Larval trematodes from marine fishes. *Jap. Jour. Zoöl.*, (3) **7**: 491–499.